DIPTERA

FAM. PROTORHYPHIDÆ, ANISOPODIDÆ, PACHYNEURIDÆ, TRICHOCERIDÆ

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WITH DESCRIPTIONS OF EARLY STAGES BY

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WITH TWO PLATES (ONE COLOURED)

INTRODUCTION

Up to the beginning of the present century the family Rhyphidæ was considered by all Dipterists to be one of the best circumscribed and most easily recognised groups in the whole order. Its essential characters were supposed to be the presence of a discal cell in the wings, combined with the absence of the « ambient vein » and of a well-market mesonotal suture, and the numerous homologous segments of the antennal flagellum. Apart from the old genus *Rhyphus*, the only genera included in the family were *Lobogaster* and *Olbiogaster*, distinguished by Osten-Sacken in 1886. But with the greatly increased attention paid during the last two decades to the Nematocerous Diptera, both larval and adult, a number of facts have come to light which have tended largely to obliterate the sharp lines of distinction which were formerly supposed to exist.

Of the greatest interest have been the results obtained from the detailed study of the larvæ. Keilin in 1912 showed that the larvæ of the genus *Trichocera*, which had till then always been placed in the family Tipulidæ, were strikingly different from those of all other known Tipulids, and further showed some most striking resemblances to those of *Rhyphus*. Keilin also demonstrated by studies carried out in 1912 (published 1919) that the resemblances between *Rhyphus* and the supposed Mycetophilid genus *Mycotobia*, to which Dufour had already called attention in 1849, were much greater and more fundamental than had ever been imagined. The question arose, were these resemblances indicative of a real relationship between the forms, or were they to be regarded as remarkable instances of convergent evolution affecting the larvæ but not the adults? Since only a few of the larval resemblances can be ascribed to independent adaptation to a similar environment, the theory of larval convergence must be to a large extent ruled out, and we must thefore conclude, not

perhaps that larval characters are more important than those of the adult for arriving at a natural classification of insects, but that all the characters of all stages should be taken into account in drawing up our classification, and that the larval characters may be of great value for this purpose. Moreover it is probable at least that in the evolution of a species changes in habit precede changes in structure, and it is during the comparatively prolonged larval period that changes in habit would seem most likely to take place and have the greatest chance of influencing the development of the species. In the case of the Culicidæ it is now well known that Dyar and Knab's classification on larval characters was found to give very different results from the usual method of classifying the adults by the structure of the palpi, and that when the adult Culicidæ were re-studied more carefully it was clearly shown that the palpal characters were quite secondary and unimportant, while more fundamental characters existed which if used in classification would give exactly the same results as the larval characters.

With the case of the Culicidæ in mind, the writer made a comparative examination of the adults of *Anisopus* (Rhyphus) and *Mycetobia*, and in 1916 was able to show that important resemblances existed between these two genera, while the supposedly fundamental difference in venation was probably of much less moment than appeared. This difference appeared to consist almost solely in the entire loss of one of the main branches of the media, which gave *Mycetobia* the appearance of a Mycetophilid fly. An exactly parallel reduction occurs in certain Tipulidæ, e. g. *Hexatoma* (as compared with *Eriocera*) and *Dicranomyia tenella* de Meijere (as compared with normal species of *Dicranomyia*). Evidence of the extent to which parallel reduction in venation may produce similar results can also be adduced from another group of Diptera : the writer has examined in the Britsh Museum collection a South African species of the Bombyliid genus *Empididelcus* (or *Hilarimorpha*) in which the venation is almost identical with that of the Mycetophilid genus *Diadocidia*.

For the purpose of the present paper a comparison has also been made between the adults of *Anisopus* and *Trichocera*. In this case however the writer has been unable to discover anything which suggests confirmation of the view of Alexander and some others that *Trichocera* should be included in the *Anisopodidæ*. In almost every respect the adults of this genus are typical *Tipulids*, but the larvæ being so very different it seems necessary to regard the genus as forming a separate family. The relationships of this family with the Anisopodidæ and the Tipulidæ are indicated below. It seems probable that we should regard *Trichocera* as a primitive genus which in its larvæ at least has retained many of the characters of the ancestors of the Tipulidæ, and its resemblances to the Anisopodidæ are probably due to this fact.

Another recent discovery of great interest is that of the genus *Axymyia* Mc Atee, for which Shannon in 1921 proposed to erect a new subfamily Axymyiinæ. In this case also the writer is not convinced that this remarkable insect should be referred to the Anisopodidæ, but as it resembles *Pachyneura* in its wing-venation it it dealt with below under Pachyneuridæ. Mc Atee's description of this genus was very brief, and referred only to the female, but through the kindness of Dr. J. M. Aldrich the writer has had the privilege of examining a male specimen of *A. furcata* taken by C. T. Greene at Great Falls, Virginia. It has therefore been possible to give a fairly complete generic description of this insect.

The latest classification of Anisopodidæ is that of Shannon, who recognises four subfamilies: Mycetobiinæ, Rhyphinæ, Axymyinæ and Trichocerinæ. As has been indicated in the above paragraphs, the present writer considers that while the first two are not fundamentally different and should not be treated as separate subfamilies, the affinities of the last two are doubtful, and they should for the present at least be kept quite separate from the Anisopodidæ and may well form two distinct families. The connections between these families and the Mycetophilidæ and Tipulidæ may perhaps be expressed by giving the writer's present idea as to the grouping of the families of

Nematocerous Diptera; the arrangement suggested is of course subject to revision. As was proposed by Malloch in 1915, a division of the Nematocera into three main groups is suggested, but the groups here indicated are by no means coextensive with those of Malloch.

I. Wings with R_{2+3} missing, though R_4 may be present. At most one anal vein distinctly reaching the margin. Ocelli present (except in some Cecidomyiidæ). Mandibles absent. Mesonotal suture absent. Larva with rare exceptions peripneustic (i. e. possessing functional lateral abdominal spiracles): never amphipneustic or metapneustic (unless in the first stage) and never aquatic.

Bibionidæ, Mycetophilidæ, Ditomyiinæ, Sciarinæ, Scatopsinæ, Cecidomyiidæ.

II. Wings with R_{2+3} present, except in a few reduced forms. At most one anal vein distinctly reaching the margin. Mesonotal suture absent or indistinct (except in Ptychopteridæ). Larva *amphipneustic*, *metapneustic* or *apneustic*, but never *peripneustic* as in group I; always with a distinct head-capsule, and generally aquatic.

A. Wings folded within the pupa, very broad, with large anal lobe; venation more or less reduced. Ocelli present or absent. Second antennal segment not enlarged. Larva apneustic.

Blepharoceridæ, Simuliidæ, Deuterophlebiidæ.

B. Wings contracted within the pupa but not folded; generally narrow, and seldom with well-developed anal lobe. Venation generally well preserved. Labrum usually well developed and chitinised. Mandibles often present, especially in the females. Ocelli absent.

1. Second antennal segment enlarged. Larva metapneustic or apneustic.

Culicidæ, Dixinæ, Chironomidæ, Ceratopogoninæ.

2. Second antennal segment not enlarged. Larva amphipneustic.

Ptychopteridæ, Tanyderidæ, Psychodidæ, Thaumaleidæ.

C. Wings contracted but not folded within the pupa, moderally broad. Ocelli present. Labrum membranous. Mandibles absent. Larva amphipneustic.

Anisopodidæ, Pachyneuridæ.

III. Wings with R_{2+3} present and generally forked; R_4 generally absent. Two anal veins reaching the wing-margin. Mesonotal suture well-marked. Mandibles absent. Usually terrestrial.

A. Ocelli absent. Larva metapneustic and without complete head-capsule.

Tipulidæ, Limnobiinæ, Cylindrotominæ.

B. Ocelli present. Larva amphipneustic and with complete head-capsule.

Trichoceridæ.

Divergent opinions have been held at different times as to the true homology of the transverse veinlet connecting the media and cubitus. According to Osten-Sacken and the earlier writes this vein was what it appeared to be, a true cross-vein to which the name « great cross-vein » was given. Later Comstock and Needham in their studies of the wing-venation of insects attempted to show that in the Tipulidæ the true medio-cubital cross vein is more or less completely obliterated, and the « great cross-vein » is really the proximal part of a branch of the cubitus, the distal part of which is apt to be fused with the media for a longer or shorter distance. This view became fairly generally accepted, and it had an apparent advantage in reducing the venation of the Diptera to one uniform plan, in which the cubitus was supposed to carry a strong distal fork. But in his recent studies on the venation of the « Panorpoid Complex », Dr. R. J. Tillyard has reverted to the idea that this vein in the Tipulidæ is the true media-cubital cross-vein, and has further suggested that in all Diptera the vein which Comstock and Needham treated as Cu_1 and which in most Dipterous families all previous authors had regarded as the upper branch of the fifth longitudinal vein, is really the lower branch of the medi-

or fourth vein; the main cubital vein being in Tillyard's view simple in all Diptera. This conclusion is largely founded on the fossil Paratrichoptera which are assumed to be the immediate ancestors of the Diptera, and strong support is certainly afforded to the view by the appearance of the venation of many craneflies, especially such genera as *Trichyphona* and *Paracladura*, also by many Tanyderidæ and Psychodidæ. For these groups there appears little difficulty in accepting Dr. Tillyard's view. But in many other families of Nematocera — Bibionidæ, Mycetophilidæ, Cecidomyiidæ, Blepharoceridæ, Culicidæ, Chironomidæ, Ceratopogoninæ — the theory of a simple cubital vein is impossible of application untess we are to admit that a breaking down of the medio-cubital connection *invariably* results in the switching over of M_4 to the cubitus, so as to make is appear as a branch of this vein. To the present writer the assumption appears entirely gratuitous that because some fossil Paratrichoptera have been found with simple cubitus (Cu_1 of Tillyard), therefore this is necessarily the case in all Diptera. It seems both easier and more reasonable to suppose that the Dipterous archetype had both a four-branched media and a two branched cubitus (Cu_1); that one of these branches proved redundant, and that evolution resulted in *either* M_4 *or* Cu_1a being lost. No living Dipteron has the complete venation postulated, but in this connection Handlirsch's genus *Mesotipula* is of special interest, as it actually has preserved (judging from the published figure) a four-branched media and a two-branched cubitus. It may well be that this genus affords us the clue to this particular problem. If this view be adopted, we may say that Cu_1 (Cu_1a of Tillyard) is lost, perhaps independently, in two groups of Nematocera: (1) The Trichoceridæ and Limnobiinæ (doubtfully in the Tipulinæ), and (2) the Tanyderidæ and Psychodidæ; probably also in the allied families Ptychopteridæ and Thaumaleidæ; while in the remaining Nematocerous families Cu_1 is preserved but M_4 lost.

The possibility remains that in *Trichocera* and the *Limnobiinæ* the « great cross vein » is really of compound origin, a short upper section of it being the true *m-cu* while the lower section is the remnant of Cu_1. That this may be the actual state of affairs is rather strongly suggested by an occasional individual anomaly which is found in some species of *Trichocera*, where a short stump is seen projecting distally from a point rather above the middle of the « cross-vein ». Further, it may be remarked that macrotrichia are of very frequent occurrence on the lower part of this « cross-vein » in *Trichocera*, though this fact may be of little significance, since *r-m* also bears macrotrichia.

In the preparation of this paper the writer has been fortunate in securing the cooperation of Dr. D. Keilin of Cambridge, who has contributed the descriptions of the larvæ and pupæ, as well as all the figures on Plate II. Without this help the paper would have had comparatively little value. The coloured figures on Plate I are from the pen of Mr A. J. E. Terzi. I would also express my indebtedness to Dr. G. Enderlein, who kindly lent all the Anisopodid material from the Berlin Museum.

Family PROTORHYPHIDÆ

This small family, of which no living representatives are known, includes a few species occurring in the Jurassic rocks of Europe. Since only the wings have been discovered, it is not quite certain that the insects are true Nematocera, the venation of *Protorhyphus* agreeing in most respects with that of the Rhagionidæ (Leptidæ), except that the anal cell is more widely open than in any living representatives of that family. However Handlirsch's supposition that *Protorhyphus* represents the ancestor of the Anisopodidæ (Rhyphidæ) seems at least equally reasonable, and we may perhaps regard this genus as the stem form which has given rise on the one hand to the Anisopodidæ and on the other to the Rhagionidæ and possibly to all other Brachycerous and Cyclorhaphous Diptera.

The main feature in which the venation of *Protorhyphus* differs from that of the Anisopodidæ is in the preservation of three branches of the radial sector. Handlirsch's genus *Eoplecia* has the radius in a very similar condition, and I therefore include it here in the Protorhyphidæ, though Handlirsch places it in the Bibionidæ, presumably on account of the reduction of the media. Study of the recent forms of Anisopodidæ has shown us clearly that the condition of the media is of much less importance than that of the radius, and these two fossil genera suggest that even in Jurassic times the media was in an unstable condition, the difference between *Protorhyphus* and *Eoplecia* being rather closely comparable to that between *Anisopus* and *Mycetobia*.

The venation of *Anisopus* is directly derivable from that of *Protorhyphus* by the suppression of R_4. On the other hand if the vein R_{2+3} is suppressed in *Eoplecia* the result is a rather close approximation to the Bibionid genus *Plecia*. In this genus, as well as in the Mycetophilidæ, it has lately been customary to regard the upper branch of the sector as R_{2+3}, but in view of the discovery of *Eoplecia* it would seem probable that in all the Bibionidæ and Mycetophilidæ R_{2+3} has been entirely suppressed, R_4 remaining in the more primitive forms. In discussing the affinities of *Mycetobia* some years ago, the writer pointed out that the Nematocera could be divided into two sections, a larger one in which the sector forks before or at the *r-m* cross-vein, and a smaller (Bibionidæ, Mycetophilidæ) in which it forks well beyond *r-m* or not at all. It may be that this fact can be explained by supposing that the first fork of *Rs* is always before or close to *r-m*, and that in the Bibionid group this first fork (R_{2+3}) is absent. This was the view of the older Dipterists (Loew, Schiner and Osten-Sacken), though Johannsen and others have referred to the short vein as R_{2+3} (second longitudinal). In that case the importance of the distinction becomes much clearer. It may be remarked that when well preserved R_{2+3} is a more or less distinctly concave vein, white R_{4+5} is convex. In *Plecia* and in the Ditomyiinæ, where the upper branch of the sector is often rather long, it is convex, suggesting that it is indeed R_4 and not R_{2+3}.

1. Genus PROTORHYPHUS, Handlirsch

Protorhyphus Handlirsch, Fossil Ins. p. 487, Pl. 43, Fig. 1 (1906).

Characters. — *Sc* ending in the costa just before the middle of the wing and well before the tip of R_1. Three branches of *Rs* present : R_{2+3}, R_4 and R_5; R_4 long and arising only a short distance beyond *r-m*. Media with three branches : M_1, M_2 and M_{3+4}; discal cell present. Cu_2 running almost straight to the margin, not distinctly hitched forward towards the tip. First anal vein present and reaching the margin well behind the tip of Cu_2: second apparently absent. (Pl. 1, Fig. 1.)

Geographical distribution.

1. *P. simplex* Geinitz, Arch. Ver. Meckl. Vol. 41, p. 61, pl. 5, f. 13 [1887] Mecklenburg (Lias).
(*Phryganidium*).
simplex Handlirsch, Fos. Ins. p. 487, pl. 43, fig. 1.
2. P. *stigmaticus* Handlisch, Schröder's Handb. Ent. Vol 3, p. 203 (1920). Mecklenburg (Lias).

2. Genus EOPLECIA, Handlirsch

Eoplecia Handlirsch, Schröder's Handb. Ent. Vol. 3, p. 203 (1920).

Characters. — *Sc* ending in the costa just beyond the middle of the wing and not far behind the tip of R_1. Three branches of *Rs* present : R_{2+3}, R_4 and R_5; R_4 rather short and arising far beyond *r-m*. Only two branches of the media present ; discal cell therefore absent. Cu_2 distinctly curved forwards at the tip. Two anal veins present, the first apparently not quite reaching the margin, the second apparently complete. (Pl. I, Fig 2.)

Geographical distribution.

1. *E. primitiva* Handlirsch, Schröder's Handb. Ent. Vol. 3, p. 203 (1920). Mecklenburg (Lias).

Family ANISOPODIDÆ

The genus *Anisopus* (*Rhyphus*) was accorded various positions among the Nematocerous Diptera by the early writers. Meigen included it, together with the genera now forming the Bibionidæ, in his tribe *Tipulariæ muscæformes*. Zetterstedt included in his tribe Rhyphii the four genera *Rhyphus*, *Ceroplatus*, *Cordyla* and *Chenesia* (*Thaumalea*), though it is difficult to imagine his reasons for making such a strange segregation. Apparently the first author to recognise the distinctness of the genus was Haliday, who in the introduction to Walker's Insecta Britannica Diptera (1851) restricted the family *Rhyphidæ* to the genus *Rhyphus* alone. In this he was followed shortly after by Rondani, and the family has been recognised as such by all dipterists since that time. As dealt with here it has rather a wider extension than that given to it by Haliday, since the genus *Mycetobia* is included, this genus having recently been shown by Keilin and the present writer to be closely related to *Anisopus* (*Rhyphus*) in spite of the different venation. A re-definition of the family characters is therefore necessary and is given below.

Although the earliest valid name for the typical genus is *Anisopus*, proposed by Meigen in 1804, yet Meigen himself in his later work as well as nearly all subsequent authors relinquished *Anisopus* in favour of Latreille's name *Rhyphus*, which was not proposed until a year later (1805). The first writer to revert to the use of the name *Anisopus* was Knab, who described some new Neotropical species under this name in 1912. Coquillett attempted to introduce the name *Sylvicola* Harris, but as I have elsewhere shown, this name should rightly be regarded as a synonym of *Rhagio* (*Leptis*). In view however of the existing rules of nomenclature the reasons for using *Anisopus* in place of *Rhyphus* seem to be irrefutable. Meigen's name *Phryne* in practically a *nomen nudum* and therefore invalid.

Characters. — The following characters are common to the adults of all the genera here included in the family Anisopodidæ :

Head somewhat flattened, or at least not distinctly produced behind ; a rather wide non-chitinised area below the occipital foramen. Ocelli present, three in number, and placed rather close together in a more or less equilateral triangle. No fronto-clypeal suture, the fronto-clypeus forming a single piece and more or less concealing the reduced and membranous labrum. Mandibles absent in both sexes. Hypopharynx free. Maxillæ with the galea well-developed but not toothed.

Maxillary palpi with a sensory vesicle in the antepenultimate segment, opening by a pore at the tip. A distinct hairy gular plate present at the base of the mentum, perhaps to be regarded as the submentum. Distinct tentorial rods present. Basipharynx rather short, with a pair of long vertical rods at its inner end, to the upper ends of which the oesophageal pump is attached, this organ narrowed posteriorly, its dorsal piece not chitinised.

Thorax with the pronotum very much reduced, especially the posterior portion, the whole pronotum divided into a pair of lateral lobes. Mesonotal praescutum not distinctly separated from the scutum, but the scutellum sharply marked off by a deep furrow. Pleural sutures distinct, especially that between the anepisternite and the sternopleurite ; a slight pit at the junction of these two pieces with the pteropleurite. Postnotum and pleurotergites large, but the latter not prominent nor divided by a furrow.

Abdomen with eight visible pre-genital segments. First tergite quite large, almost as large as the second, and with a pair of prominences or blunt tubercles at the base. Second segment not elongate, without shining transverse pits. Eighth segment small. Anal segment well developed, the tergal portion with a pair of nearly free cerci in the male as well as in the female. Aedeagus complicated and strongly chitinised.

Legs only moderately long. Posterior coxæ short, the front pair rather longer. Front tibiæ with one spur, middle and hind pairs each with two, the spurs finely pubescent; no strong bristles. Claws all alike and simple. Pulvilli absent. Empodia (when present) hairy. Wings rather broad, with a well developed anal lobe and a well-marked re-entrant angle between the anal lobe and the squama, the alula being more or less indicated. Costal vein ending at or a little beyond the tip of R_{4+5}. Subcosta long and ending in the costa about the middle of the wing, well beyond the base of *Rs*; subcostal cross-vein absent. Stem of radius straight, not sinuous below the humeral cross-vein, but with a slight interruption in this position. Arcular cross-vein present. Radial sector arising near the middle of the wing, with two branches, the upper (R_{2+3}) quite long and concave, occupying the furrow between R_1 and R_{4+5}, and ending at most a short distance beyond the tip of R_1: lower branch (R_{4+5}) long, convex, and ending close to the tip of the wing. Radio-median cross-vein situated slightly or distinctly beyond the fork of *Rs*. Media with not more than three branches, M_4 being absent. According to Tillyard's interpretation the media is four-branched and Cu_1 simple, the *m-cu* cross-vein being the piece here considered as the base of $Cu_1 a$. See discussion of this point in the introduction to this paper. Main stem of the cubitus (Cu_1 of Tillyard) forked distally, the lower branch of the fork slightly or distinctly curved upwards or forwards towards the tip. The lower concave branch of the cubitus (Cu_2 of Tillyard) rather weak and not reaching the wing-margin. First anal vein distinct and reaching the margin. Second anal (axillary) vein present but evanescent apically. Cross-vein connecting the two anal veins indistinct and close to the base of the wing. Squama fringed.

Early stages. — The early stages of *Mycetobia* and *Anisopus* have been studied in some detail by Keilin, who has given a most interesting comparison between the characters common to these two genera and those exhibited by the larvae of the Mycetophilidæ. His list of characters forms an admirable definition of the family characters of the Anisopodidæ, and is as follows:

Characters common to Mycetobia pallipes and Rhyphus fenestralis.

1. The eggs are invested with a gelatinous mass which is fixed to a solid substratum.
2. Eggs are pear-shaped.
3. Embryo in the egg curved.
4. The larvæ move in a serpentine manner, or by means of very active mandibles.
5. The segments of the body (abdomen) are separated by intercalary rings.
6. The larva head with a pair of tentorial rods similar to those of larvæ of *Trichocera*.
7. Antennæ with a special sensory organ corresponding to the bell-shaped papilla of many other dipterous larvæ (for instance, those of *Ditomyia* and all Cyclorhaphous Diptera) and with some small cylindrical papillæ.

Characters common to all the Mycetophilidæ except the genera Ditomyia and Symmerus.

1. Eggs are more or less scattered an the surface of the fungus or rotten wood.
2. Eggs are elongated or sub-spherical.
3. Embryo straight.
4. The larval movements are worm-like.
5. No distinct intercalary wings; only some larvæ — for instance, those of *Ceroplatus* — have the segmentation of their abdomen masked by superadded transversal folds.
6. Head without tentorial rods.
7. Antennæ either elongated as in *Bolitophila*, or reduced to a flat, wide, non-chitinised surface bearing some very small sensory papillæ.

8. Mandibles show two distinct portions : basal portion with an internal hook, and terminal or apical portion which is more chitinised, ending in three teeth and bearing two brushes of brown setæ.	8. Mandibles flattened, strongly chitinised, and with their internal margin toothed.
9. Maxillæ fleshy and soft; the maxillary palp broad, thick, transparent, bearing two groups of sensory papillæ ; the internal part of the maxillæ, besides a few sensory organs, bears numerous long setæ.	9. Maxillæ flattened and strongly chitinised, with their internal margin toothed, like those of the mandibles. The maxillary palps are very much reduced.
10. Labrum with two mid-ventral protuberances covered with hairs, and a small comb-shaped plate on each side of posterior protuberance.	10. Labrum without mid-ventral protuberances and without comb-shaped plates.
11. Labium well-developed and with distinct labial palps.	11. Labium reduced and not visible from exterior.
12. The thoracic sensory organs which are the remains of the thoracic legs are composed of four hairs (two long and two short).	12. Thoracic sensory organs composed of four hairs of equal length.
13. Respiratory system is amphipneustic, with only two pairs of functional spiracles: (1) prothoracic and (2) postabdominal.	13. Respiratory system is either hemi-pneustic, with one pair of prothoracic and seven pairs of abdominal spiracles, or propneustic (*Polylepta* or *Diadocidia*) or apneustic (*Ceroplatus*).
14. Alimentary duct without anterior cœca.	14. Alimentary duct with a pair of anterior lateral cœca.
15. Anus ventral.	15. Anus terminal or subterminal.
16. Salivary glands short.	16. Salivary glands very long.
17. Hypoderm of posterior segments of larvæ, which surrounds the anal cleft, is composed of very large and thick cells.	17. No special large cells in hypoderm of the posterior end of the body.
18. Pupæ strongly chitinised, with rows of sma hooks on the abdominal segments and especially on the posterior end of the body.	18. Pupæ with thin chitin and without the *rows* of short spines or hooks.

« All these characters show as clearly that the difference between the larva of *Mycetobia* and those of *Mycetophilidæ* (s. l.) is as striking as its resemblance to the larvæ of Rhyphidæ. »

Most of the characters listed above apply also to the genus *Olbiogaster*, but in this genus there are some very important differences, particularly in regard to the structure of the mouth-parts and antennæ, as indicated in Keilin's diagnosis below. If larval structure is a safe guide to classification, it is evident that *Olbiogaster* is much less closely related to *Anisopus* than is *Mycetobia*. This conclusion, it is important to note, would also be reached if we regarded the thoracic bristles and the hind tibial comb of the adult as of greater significance than the venation.

Habits. — The early stages of four of the five genera are more or less known, and are passed in situations where there is plenty of wet decaying and fermenting organic matter, which forms the food

of the saprophagous larvæ. These situations may be merely sodden or may be actually under water; the larvæ are able to swim actively as well as crawl, and so long as they have occasional access to the air the amount of water present is immaterial. Keilin has described the peculiar manner in which the complicated mandibles are used for locomotion. Pupation takes place in the larval habitat, without the formation of any cocoon; the pupæ wriggle rather actively and before the emergence of the adult make their way to the surface. Some of the habits of the adults are discussed under the genus *Anisopus*; in regard to the other genera practically nothing has been recorded.

Geographical distribution. — See under the genera *Anisopus*, *Olbiogaster* and *Mycetobia*.

KEY TO THE GENERA OF ANISOPODIDÆ

1. *Media three-branched, discal cell present* . . . . . 2.
   Media two-branched, discal cell absent; hind tibiæ with comb . . . . . 4.
2. *Wing-membrane with macrotrichia, at least towards the tip; hind tibiæ with comb* . . Genus Anisopus.
   Wing-membrane devoid of macrotrichia; hind tibiæ without comb . . . . . 3.
3. R_{4+5} *ending well before the wing tip, eyes densely hairy* . . . . . Genus Lobogaster.
   R_{4+5} *ending only a little before the wing tip, eyes nearly bare* . . . . . Genus Olbiogaster.
4. R_{2+3} *ending in the costa* . . . . . Genus Mycetobia.
   R_{2+3} *ending in* R_1 . . . . . Genus Mesochria.

1. Genus ANISOPUS, Meigen

Phryne Meigen, Nouv. Class. Mouches [1800] (no species).

Anisopus Meigen, Illiger's Mag. Vol. 2, p. 264 [1803] (no species); and Klassif. Vol. 1, p. 102 (1804).

Rhyphus Latreille, Hist. Nat. Crust. Ins. Vol. 14, p. 291 (1805).

? Asarcomyia Scudder, Fossil Ins. N. Am. Tertiary, p. 567 (1890).

Characters. — Eyes with a rather scanty and very short pubescence; well separated in the ♀ but more approximate and often actually in contact in the male. Ocelli rather large, placed on a distinct tubercle. Head somewhat flattened behind and rather bristly on the vertex; face gently convex, always wider than the front and quite bare. Antennæ not longer than the head and thorax together, those of the male scarcely longer than those of the female; scape moderately long, the first segment longer, the second as long as broad. Maxillary palpi with four distinct segments (apart from the rudimentary palpiger), the second segment the longest and usually much swollen, especially in the ♀; third segment quite short, much shorter than the fourth; the third and fourth pendent. Labium projecting forwards in repose, with a very well-marked glossa between the two labella. Pronotum much reduced, not visible dorsally. Mesonotum with scanty fine hairs and with longer bristly hairs about the root of the wings and in two dorsocentral rows, these being much longer and more conspicuous in some species than in others. Scutellum generally with a pair of bristles or bristly hairs. Meron large and distinctly marked off from the middle coxa; epimeron broad. Abdomen more or less cylindrical in the male, without flat lateral expansions of the tergites; shorter and broader and blunt-ended in the female. Hypopygium small and more or less retracted; anal segment in the normal dorsal position, with a large flat ventral plate, separating it completely from the genitalia; ninth sternite greatly developed; claspers (gonostyles) placed towards the inner side of the side-pieces. Aedœagus of complicated structure and ending internally in an extremely long coiled

capillary tube. Hind tibia with a well-marked apical comb on the inner side. Empodium large in the female, very large in the male. Wings with numerous macrotrichia on the membrane on at least the apical third. Costal vein ending practically at the tip of R_{4+5}. R_{2+3} rather strongly sinuous, ending well beyond the tip of R_1; the cell R_1 somewhat widened before the tip, its apical part occupied by a conspicuous stigma. Media three branched; discal cell present; cross-vein *r-m* a little beyond the middle, *m-cu* far before the middle of the discal cell; cells M_2 and M_3 of approximately equal width at the wing-margin. Squamal fringe long (**Pl. 1, Fig. 3**).

« **Pupa** (**Pl. 2, Fig. 4**). — In *A. fenestralis* the pupa is 8.5 mm. long; the prothoracic horns are small and sessile; the three pairs of legs are superposed; the head bears a pair of long anterior hairs; there are four pairs of shorter hairs on the dorsal and dorsolateral aspects of the thorax. Each abdominal segment, near its posterior border, shows a circlet of small hooks, some of which at regular intervals bear a long sensory hair. The posterior end of the pupa is provided with 7 pairs of strongly chitinised hooks.

» **Larva.** — The larva of *A. fenestralis* Scopoli (**Pl. 2, Fig. 1-3**), is 12-14 mm. long, composed of a head capsule, 3 thoracic and 8 abdominal segments; the latter show a series of supplementary or intercalary rings. The 8th abdominal segment is divided into 5 secondary rings, the last terminating in 5 fleshy lobes bordered by a fringe of small setæ (**Fig. 2**). The anus lies ventrally between the 1st. and 2nd. ring of the terminal segment, and is surrounded by a special shield-like thickening (*a. s.*), lined by very large hypodermal cells. The thoracic segments show a very characteristic pigmentation. The *respiratory system* is amphipneustic; the prothoracic spiracles are composed of 3 spiracular papillæ; the post abdominal, lying between the lobes of the last segment, are crescent-shaped and are composed of 23 papillæ or clefts. The *head capsule* (**Pl. 2, Fig. 3**) is completely free; strongly chitinised dorsally; white, thin and soft ventrally. The ventral surface of the head in its anterior region is covered with several rows of hair-tufts. The *antennæ* are only visible dorsally; they are small and composed of a strongly chitinised basal segment bearing a transparent mushroom-like sensory organ (corresponding to the bell-shaped organ of other Dipterous larvæ) and a series of small sensory papillæ. The *labrum* (*lr*) forms a fleshy ventral thickening covered with setæ. Posteriorly it shows two chitinous bands each covered with a comb-like chitinous process (*cm*). Between the combs lies a second medio-ventral cushion-like lobe (*pr*) covered with sensory papillæ and ordinary chitinous setæ. The *mandibles* are composed of two distinct portions : 1) a large basal portion bearing at its distal end a chitinised dentate process (*v. h.*); and 2) a terminal strongly chitinised portion (*m. d.*) ending in two teeth and bearing brush-like groups of setæ. The *maxillæ* are soft and composed of two portions : 1) the maxillary palp bearing two sensory vesicles (*a* and *b*) each composed of several papillæ, one small sensoryp it, one sensory hair and a fringe of numerous setæ; and 2) the maxillæ proper (*mx*), which in addition to a few sensory papillæ are covered, near their anterior border, by numerous brown flexible setæ. The *labium* or prementum of de Meijere is soft, bordered by a fringe of setæ, and bears two circular sensory organs composed of several small papillæ. The tentorial rods are clearly seen by transparency. The *alimentary* canal is simple, without cæca. The *salivary glands* are simple and short.

» The larva of *A. punctatus* Fabricius differs from the previous species by the very characteristic dark markings, which extend over all the segments of the body. The last abdominal segment (**Pl. 2, Fig. 5**) is short and *not* divided into 5 rings; the perianal shield-like thickening is simple, with the anus lying near its posterior border; the perispiracular fleshy protuberances are also much shorter than in *A. fenestralis*. *A. picturatus* Knab differs from *A. fenestralis* in having the perianal shield more elongate and extending further towards the dorsal surface of the segments.

» **Eggs.** — The eggs of *A. fenestralis* are pear-shaped and embedded in a jelly-like substance; the embryo when fully formed is curved inside the egg. » (Keilin.)

Habits. — Larvæ of the genus *Anisopus* have been found in a great variety of situations, but always in the presence of fermenting organic matter. *A. punctatus* breeds commonly in the dung of farm animals, especially cows, and in the liquid running from farmyard manure heaps. *A. fenestralis* sometimes occurs also in these situations, also in fermenting sap running from wounds in trees, in water in tree-holes, in the decaying roots of plants such as *Arctium* and *Angelica*, and in other such situations. One of the most remarkable breeding-places of *A. fenestralis* which has come to the writer's notice was in a specimen of liver belonging to the London School of Tropical Medicine. The liver had been preserved in 10 % formalin for 7 years, after which the jar was opened and the liver being partly exposed to the air (through still in the formalin) became covered with mould and was then attacked by *A. fenestralis*. Another insect was also present which I suspect to have been *Mycetobia pallipes*, although the larvæ were not found and the adults escaped before positive identification was made. It is of interest to note that *M. pallipes* has on several occasions been found breeding in company with *A. fenestralis*. The most remarkable life-history of a member of this genus so far known is that of *A. picturatus*, whose larvæ were found by Picado in the leaf-bases of Bromelias, and like many other insects occupying this habitat they exhibit some amount of adaptation to their restricted surroundings.

Although the species of *Anisopus* can hardly be considered as of any economic importance, Theobald has placed on record a case of damage to bee-comb caused by *A. fenestralis*, and complaints are occasionnally received at the British Museum of the larvæ being found in cyder or home-made wine.

The males of some species if not of all perform the combined aerial dances which are so commonly executed by male Diptera of various families, the dancing swarms usually being found on the lee side of trees and bushes, often under overhanging branches. In the case of *A. fenestralis* the swarms contain only a few individuals, at least according to the writer's experience, but in the case of *A. punctatus* the swarms are often very large. This difference is possibly connected with the larger size of the eyes in the latter species. Mating takes place by a female flying into the swarm. Details as to the mating and egg-leying processes, and as to the feeding-habits (if any) of the adults have not been placed on record. Nothing very definite is known either as to the method of overwintering practised by the different species. It is doubtful whether true hibernation occurs, but females of *A. fenestralis* are certainly not infrequently seen during the winter months and probably survive during a part at least of the winter. The writer has noted a rather conspicuous difference in the sitting postures of *A punctatus* and *A. fenestralis*, the former species resting with the fore part of the body raised, while in the latter it is the hind part which is slightly raised.

Geological distribution. — Although a fossil from the Purbeck rocks of England has been described as *Rhyphus priscus*, no undoubted species of *Anisopus* has yet been described from an older formation than the Eocene. It seems probable that Scudder's *Asarcomyia cadaver*, from the North American Eocene, may be a species of *Anisopus*, and several species have been described from Baltic Amber and other Tertiary formations of Europe. Loew reports having observed three species in Baltic Amber, and theBritish Museum has recently acquired specimens of these three supposed species from his collection. They prove on examination to be one and the same, and are evidently Meunier's *R. thirionis*. They very closely resemble the existing European *A. punctatus* (7), the wing-markings and venation being the same and the male eyes touching. If they are to be distinguished from the living species it can only be by their rather smaller size and a small difference in genitalia, which cannot be satisfactorily defined in the fossils. Heer's *R. maculatus* on the other hand appears to represent the living *A. fenestralis*, the wing-markings being almost identical.

Geographical distribution. — Members of this genus are found in nearly all parts of the world, but most abundantly in the Oriental and Neotropical regions. Until recently no endemic species was known from Africa, though during the preparation of this revision one such has been received for determination from the Berlin Museum. A specimen of what appears to be the common *A. fenestralis*, has also been received from Dar-es-Salaam, where it has no doubt been introduced. The paucity of species of *Anisopus* in the whole Ethiopian region (none having yet been found in Madagascar) is surprising and not easily explained. The species are also few in number in Europe and North America. They are remarkbly uniform in structure, the most conspicuous differences being in the male eyes, but examination of a number of species shows that holopticism of the male is only a secondary phenomenon, and that a truer idea of the relationships of the species can be obtained from a study of the small differences which occur in wing-markings and venation. One point of general interest may by mentioned, that is the evident relationship between the New Zealand species *A. notatus* and *A. undulatus*, and the Chilean *A. fuscipennis*. The only group which it might possibly be justifiable to regard as forming a distinct subgenus is that of the species with ringed antennæ, including the African *A. annulicornis* and three Oriental species.

KEYS FOR DISTINGUISHING THE SPECIES OF ANISOPUS

Palæarctic and Nearctic species.

The palpi are mostly or all black in all species known from these regions.

1. *Cell* M_1 *pointed at the base; tip of wing clear* . . . . . 2.
   Cell M_1 *broad at the base; tip of wing with distinct markings* . . . . . 4.
2. *Cell* R_5 *quite clear* . . . . . FUSCATUS Fabricius.
   Cell R_5 *with a dark cloud near the base* . . . . . 3.
3. *Ninth sternite of male with a pair of black processes* . . . . PUNCTATUS Fabricius.
   These processes absent . . . . . MARGINATUS Say.
4. *Two dark areas in the upper basal cell (inner one sometimes faint); preapical costal spot conspicuously white; middle stripe of thorax divided* . . . . . 5.
   At most one dark area in the upper basall cell; preapical costal area not conspicuously white; middle stripe of thorax entire . . . . . 6.
5. *Palpi yellow at the base* . . . . . SUZUKII Matsumura.
   Palpi all black. . . . . . ALTERNATUS Say.
6. *Wing-markings reduced, the upper basal cell quite clear.* . . LIMPIDUS Edwards.
   Wing markings more distinct, a dark cloud in the upper basal cell (sometimes faint in the ♂) . . . . . 7.
7. *Hind femora yellow except at tip; male eyes almost touching.* . ZETTERSTEDTI Edwards.
   Hind femora with a more or less distinct dark median ring; male eyes well separated . . . . . 8.
8. *Cell* R_1 *dark except at base* . . . . . CINCTUS var. WITHYCOMBEI Edwards.
   Cell R_1 *with a yellow area beyond the middle.* . . . . . 6.
9. *Tip of ninth sternite of ♂ broad and black* . . . . . FENESTRALIS Scopoli.
   Tip of ninth sternite of ♂ narrow and not blackened. . . . CINCTUS Fabricius.

Palæotropical species.

1. *Flagellum of antennæ with pale rings* . . . . . 2.
   Flagellum of antennæ all dark . . . . . 5.